

Light, Vernal Earl

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PHOTORECEPTORS IN MYA ARENARIA, WITH SPECIAL REFERENCE TO THEIR DISTRIBUTION, STRUCTURE, AND FUNCTION ¹

V. EARL LIGHT

Zoölogical Laboratory, Johns Hopkins University

SEVEN TEXT FIGURES AND ONE PLATE (ELEVEN FIGURES)

AUTHOR'S ABSTRACT

Experimental studies on the responses to light in *Mya arenaria* L. indicate that photosensitive tissue is located somewhere near the inner surface of the siphon and that the siphon is sensitive throughout its entire length.

A histological study of the siphon shows cells of a special type in the photosensitive region, which are most abundant where the inner surface of the siphon is most sensitive. They are found throughout the length of the siphon, just beneath the inner epithelial layer, around both the incurrent and excurrent siphons. They receive nerve elements from branches of sixteen large nerves.

Each cell contains a characteristic inner structure, the optic organelle, composed of a rather large hyaline structure, the lens, which is surrounded by a network of nerve fibrillae, the retinella. Light rays, reflected from a flat mirror through the lens in these cells, are brought to a focus in the region of the retinella, irrespective of the direction of the rays.

The cells are similar in structure and function to visual cells in leeches and photoreceptors in the earthworm. Available data indicate that they function as photoreceptors and that the fibrillae of the retinella are direct receptors of light stimuli.

Pigment spots found in considerable number on the distal third of the siphon, and thought by some to be eyespots, are, owing to simulation of the background, probably protective in nature, rather than functional in photoreception.

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INTRODUCTION

Poli (1795) was probably the first to maintain that some of the lamellibranchiate molluscs possess eyes. He pointed out that *Ostrea* (*Pecten*) *jacobaea* and *Spondylus gaederopus* possess small bright structures distributed along the edge of the mantle in considerable numbers, and he asserted that these structures are eyes. Since then eyes have been found and studied in various bivalve molluscs by Krohn ('44), Siebold ('48), Hensen ('65), Gegenbaur ('78), Sharp ('83, '84), Carrière ('85, '89), Patten ('86), Thiele ('89, '90), Retzius ('92), Hesse ('00), Küpfer ('16), and others. In some forms, e.g., *Pecten*, *Arca*, *Spondylus*, *Lima*, and *Pectunculus*, the eyes are well developed. In others, e.g., *Solen*, *Venus*, *Cardium*, *Mactra*, and *Mya*, the presence of eyes is questionable, as indicated by the following.

Will ('44) states that in *Cardium*, at the tip of each of the thread-like tentacles, projecting from the distal end of the siphon, there is a sunken eye; but Carrière ('85) says that these structures are not eyes, and Leydig ('57) contends that he could not find any eyes in other similar molluscs. Ryder ('83), however, holds that in *Mya arenaria* there are, near the free end of the siphon, pigmented papillae which serve as eyes. He says: "do not the habits of *Ostrea*, . . . justify us in expecting to find rudimentary organs on the mantles

and siphons of molluscs, answering the purpose of eyes, as appears to be the case in the instance of *Solen*?"

However this may be, it has long since been known that many molluscs in which no eyes are evident respond very definitely to light. These responses have been studied more extensively in *Mya arenaria* than in any other related form, especially by Wenrich ('16), Hecht ('19, '20), Piéron ('25, '26), and Folger ('27), but these investigators did not consider the sensory structures involved in the responses. The present investigation was undertaken to ascertain the location, the nature, and the function of these structures. The conclusions reached are based upon a study of the response to light under various conditions and upon a histological study of the siphons.

MATERIAL AND METHODS

This investigation was begun at the Marine Biological Laboratory at Woods Hole and continued at The Johns Hopkins University. The specimens used at Woods Hole were furnished by the supply department of the laboratory. Those used at The Johns Hopkins University were obtained from sand bars in that portion of the Severn River called Round Bay, about 6 miles up the river from Annapolis.² An abundance of specimens was collected here at different times and taken to the laboratory.

A dozen or more of the individuals from the first collection were put into a large aquarium containing sand, water, and plants from the same locality, after which the water was aerated. In this collection there was one specimen much smaller than the rest. This one, with two other small molluscs of a different species, brought into the laboratory at the same time, was put into a battery jar together with débris and water. The water was not aerated, and no particular

² The animals in this region have very brittle shells, probably owing to deficiency in calcium, so that in obtaining them special precautions must be taken to avoid crushing them.

attention was paid to it for some time. The specimens in the aquarium all died within three weeks, while at the end of six weeks the three animals in the battery jar were still alive, and appeared to be in good condition. Fewer animals, which had just been collected, were now put into the same large aquarium with a fresh supply of water, sand, and plants. These animals lived slightly longer than the first group, but not as long as desired. It occurred to me, then, that perhaps the aerated specimens were receiving too much oxygen. Other specimens were therefore procured and put into individual battery jars, each containing brackish water, sand, and water plants, but the water was not aerated.

TABLE 1

Length of life in Mya arenaria under laboratory conditions. Thirty-eight specimens used

		NUMBER OF ANIMALS THAT DIED DURING EACH OF THE FOLLOWING THIRTY-DAY PERIODS										
		1 to 30	31 to 60	61 to 90	91 to 120	121 to 150	151 to 180	181 to 210	211 to 240	241 to 270	271 to 300	Total number
Date collected	Dec. 10					2		1		1		4
	Feb. 25	4	2	1	3	1	3	1			1	16
	Apr. 21	1	2	3		3	3	3	3			18
Total		5	4	4	3	6	6	5	3	1	1	38
Average length of life in days		19	43	65	117	134	159	187	220	241	294	125

Kellogg ('99) maintains that adult *Mya* die quickly in the laboratory. Some of the specimens in the battery jars, however, lived more than eight months. The approximate length of life of thirty-eight specimens, collected at three different times, is recorded in table 1. By referring to this table one will see that two animals remained alive under laboratory conditions for a period exceeding eight months, and that one of these lived over nine months. This individual, collected February 25th, had about three-fourths of the siphon removed

by an operation September 25th. The animal recovered successfully from the effects of the operation, and lived until December 15th—a period of 294 days. The average length of life of all the specimens was 125 days; twenty-two lived longer than the average, while only sixteen did not live as long as the average, and the greatest mortality occurred during the first thirty-day period, in the group of animals gathered February 25th. This high mortality can be attributed to two factors: February 25th was a very cold day, and some of the animals were injured in digging them from the partly frozen sand bar. Then, too, large numbers of specimens of the crustacean *Gammarus* were brought into the laboratory and put into the jars with the molluscs. This crustacean is a scavenger, and it was thought that it would eat the dead and decaying plant and animal life which gathered in the aquaria. This proved to be true, but it also attacked the molluscs, and caused the death of several of them.

THE DISTRIBUTION OF PHOTSENSITIVE TISSUE AS INDICATED
BY RESPONSE TO LIGHT UNDER VARIOUS CONDITIONS

A. Normal animals

Nature of response. *Mya arenaria* responds both to an increase and to a decrease in luminous intensity. Wenrich ('16) maintains that a different set of muscles is involved in the reaction under the two conditions. He says:

For decreases in intensity the movement was that of the muscles involved in closing the siphonal openings, while in responses to increases, the siphon tubes were withdrawn. In the latter case the withdrawal of the siphon tubes was sometimes accompanied by closure of the openings, especially if the reaction was a vigorous one, but as a general rule, when the movement of the siphon tube was not great, no closure of the openings resulted.

In the following observations responses to increase of intensity only are considered. These responses consisted in withdrawal of the siphon, and often closing of the siphonal openings, in accord with Wenrich's statement. But usually

only the tip of the siphon contracted; the proximal two-thirds moved little or not at all, and after a response the animal usually soon recovered and extended the siphon to its former position. The period between illumination and the beginning of contraction is known as the reaction time.

Response to localized photic stimulation. A device for projecting a small beam of light was constructed in order to ascertain the location of photic sensitivity in the siphon and other parts of the animals. This was done by placing a Ford headlight bulb, connected to three dry cells, in a light-tight box attached to the tube of a microscope (Patten, '15). A wooden block with a small circular aperture at the center was placed in the tube of the microscope about 1 inch from the light. A similar wooden block was also placed near the lower end of the tube where the objective was attached. With this arrangement of light and screens, it was possible to obtain a minute beam of rather intense light.

In order to obtain illumination of approximately the same intensity and the same size of field in each test, a thin wire was attached rigidly to the objective of the microscope tube. This wire was made of such length that when the point was brought close to an object, the area illuminated was about 1 mm. in diameter. The wire was adjusted so that the tip coincided with the outer edge of the circular area illuminated.

For use in the experiments made to ascertain the relation between response and localized photic stimulation, a group of thirty-one animals of various sizes was selected; then each animal was put into a battery jar in the laboratory, containing just enough water from the stock aquarium to cover it. Five or six of these battery jars were now taken into the dark-room and placed on a table, at intervals of about a foot and a half, after which each one was covered with a light-tight box and left for from two and one-half to three hours for dark adaptation. Then, with the room in darkness except for just enough light, supplied by a ruby lamp,³ to enable

³ It was found that the animals did not at any time respond to the illumination produced by the ruby lamp.

objects to be discernible, the light-tight cover was carefully removed from one of the jars; after which the device for projecting a small beam of light, described above, was adjusted for stimulation of the base of the siphon. Then the light in the apparatus was turned on, and at the same time a stop-watch was started. The watch was stopped at the instant the siphon began to contract in response to the stimulating light. The time was then recorded, after which the light-tight box was again placed over the jar. In this way each of the rest of the five or six animals in the dark-room was subjected to localized photic stimulation at the base of the siphon, then the process was repeated for each of the animals, with the stimulation located elsewhere.

In this manner, the relation of response to localized photic stimulation was ascertained for the projecting foot; the edge of the mantle; the outer surface of the siphon at base, middle, and tip; and the inner surface of the incurrent and the excurrent siphons.⁴ It required about ten minutes for one test of each animal in the group, so that a period of dark adaptation of ten minutes intervened between two successive stimulations of the same animal.

After the observations of the animals in this group were completed, another group of five or six individuals was taken into the dark-room and observations made on them in the same way. This procedure was continued until the thirty-one animals selected were tested.

No responses were observed when the edge of the mantle or the projecting foot was illuminated as described. The results obtained by illuminating other regions are presented in table 2. By referring to this table the following will be seen:

The entire siphon in *Mya arenaria* is sensitive to lateral photic stimulations, but the tip is most sensitive. Of the

⁴In the smallest animals the siphon was so small and so nearly transparent that it was impossible to see any specific difference in the localization of the stimulus dependent upon direction of illumination. Only results obtained for lateral illumination are therefore recorded for these.

thirty-one specimens tested, twenty-four responded to stimulation at the tip, twelve to stimulation at the middle, and nine to stimulation at the base. The base of the siphon is, however, only slightly sensitive, for although nine individuals of

TABLE 2

Relative photic sensitivity of different parts of the siphon in Mya arenaria; area illuminated, 1 mm. in diameter; intensity, 12.4 m.c.

DESIGNATION OF SPECIMEN	LENGTH OF SHELL IN CM.	LENGTH OF EXTENDED SIPHON IN CM.	REACTION TIME (IN SECONDS) WITH ILLUMINATION					
			Of outer surface at			Of inner surface of		
			Base of Siphon	Middle of siphon	Tip of siphon	Incurrent siphon	Excurrent siphon	Parts of both siphons
23	10.0	7.0	N	6.0	4.0	3.5	3.7	3.6
1	9.0	8.0	N	N	5.0	2.0	4.0	3.4
26	8.0	12.0	N	N	N	—	—	4.0
24	6.5	1.0	N	C	N	C	C	C
2	6.0	6.5	N	N	N	3.2	—	—
3	6.0	4.0	N	N	3.2	—	—	2.8
21	6.0	7.0	N	N	N	N	N	2.2
27	6.0	8.0	N	N	C	C	C	C
29	5.5	6.0	N	N	3.2	—	—	2.6
25	5.5	12.0	N	N	N	C	C	C
10	5.5	6.0	N	N	2.4	1.8	2.0	—
9	5.5	5.0	N	9.8	3.8	3.4	3.4	4.0
6	5.5	4.0	N	N	2.4	3.6	3.0	4.0
11	5.0	7.0	N	N	3.8	—	—	2.4
12	5.0	3.5	N	4.0	3.1	—	—	2.5
22	5.0	3.5	4.2	N	2.4	—	—	2.2
28	5.0	7.0	N	N	3.0	—	—	C
7	4.5	0.0	—	—	—	—	—	—
8	4.5	8.0	N	4.2	4.0	—	—	2.4
14	4.0	1.5	3.4	3.0	2.8	C	C	C
18	3.5	3.5	6.6	C	3.0	C	C	C
17	3.5	1.5	2.4	3.6	2.0	—	—	1.6
4	3.3	3.0	5.0	4.0	3.0	—	—	2.4
16	3.0	3.5	N	3.8	2.8	—	—	2.0
15	2.5	3.5	N	N	2.8	—	—	2.8
5	1.4	.75	N	1.6	1.4	—	—	1.6
30	1.1	.5	1.8	2.1	2.0	—	—	—
19	1.0	.5	1.6	1.5	1.5	—	—	—
20	1.0	.3	C	1.5	1.3	—	—	—
31	1.0	.4	1.4	C	1.2	—	—	—
13	.75	.3	1.4	C	1.4	—	—	—

N, no response; C, siphon closed; —, not stimulated.

the group responded, the reaction time varied greatly, and it was obtained only in the small animals, which are in general more sensitive than large ones. The response to stimulation is more rapid when the inner surface of the siphons is illuminated than when the outer surface is illuminated, the reaction time being shorter in all but three of the specimens tested, and in these three there was very little difference. The inner surfaces of the incurrent and the excurrent siphons are approximately equally sensitive. No response to localized photic stimulation is obtained when the siphons are closed.

The fact that the reaction time is shorter when the inner surface of the siphon is illuminated than when the outer is illuminated seems to indicate that the photosensitive tissue is located somewhere near the inner surface. Since, however, the results were obtained only in one intensity of illumination and with but a small area illuminated, they cannot be considered conclusive. Consequently, a similar study was made, extending over a wide range of luminous intensities, with larger areas illuminated.

Response to light of different intensities with large areas illuminated. All work on the reaction of *Mya* to light of different intensities was performed by means of apparatus arranged as illustrated in figure 1. In a dark-room a 1000-watt, concentrated filament, projection, Mazda lamp was mounted in a ventilator shaft (containing an opening 4 cm. square), in such a way as to produce a horizontal beam of light (fig. 1, A); and a 500-watt lamp was mounted in a light-tight box (also containing an opening 4 cm. square), in such a way as to produce a vertical beam of light (fig. 1, B). Various intensities of light were obtained by the use of a series of Wratten neutral-tint filters placed in the path of the rays of light. The different filters in this series transmitted, respectively, 0.01, 0.0476, 0.1, 1.0, and 10.3 per cent of the incident light. The voltage of the current used was frequently adjusted with a rheostat in the circuit, but in spite of this it varied considerably, resulting in a corresponding variation in the intensity of the light used. However, the maximum varia-

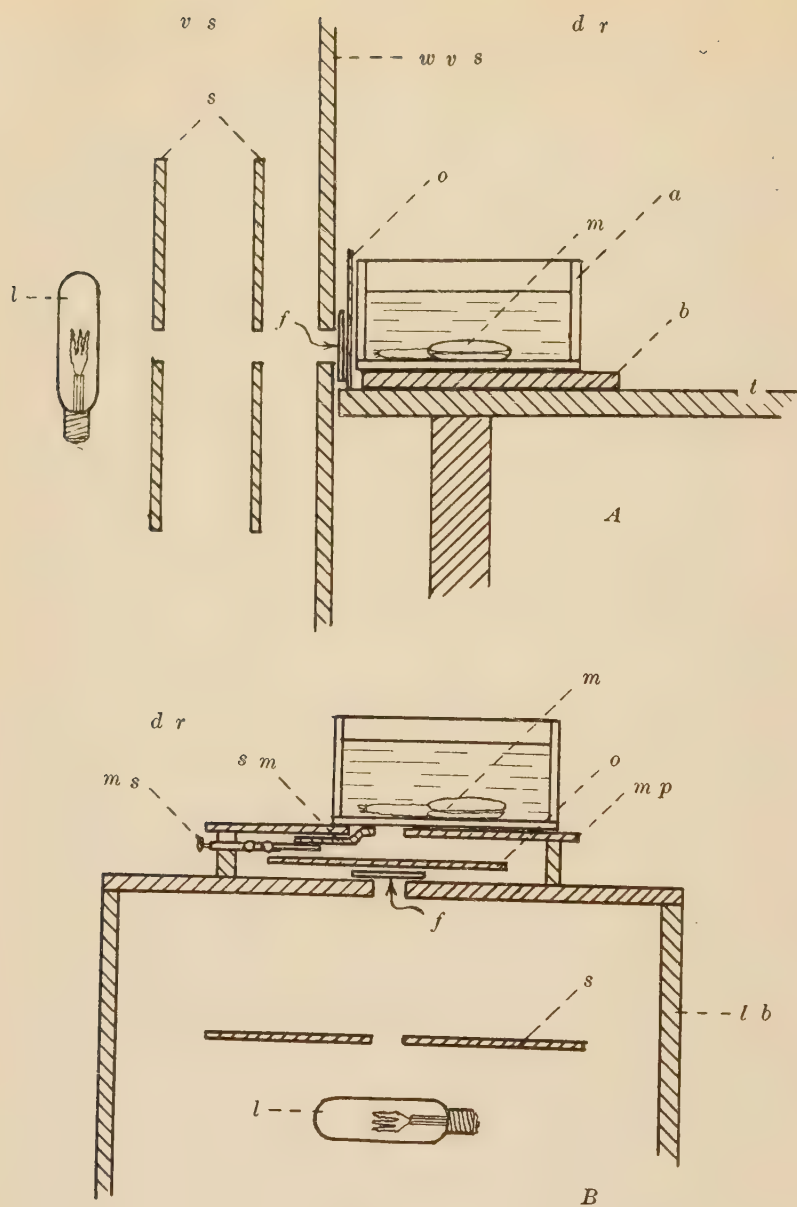


Figure 1

tion from that recorded in the tables never exceeded 12 per cent, and that obtained in only a few tests.

Each of six animals selected was taken from its battery jar in the laboratory and put into a small rectangular, plate-glass aquarium containing sufficient water from the battery jar to cover it. Then the animals were put upon a table in the dark-room, faintly illuminated with light from a ruby lamp, covered with light-tight boxes, as in the previous experiments, and left for two and one-half hours, i.e., until they were thoroughly dark adapted, after which the light-tight box was removed from one of the animals, and the aquarium containing it carefully transferred to a position before the opening in the wall of the ventilator shaft and so arranged that the distal end of the siphon was directed toward the lamp (fig. 1, A). The densest Wratten filter and an opaque screen were now placed between the source of light and the aquarium containing the animal. Then the light was turned on, and after it had attained its maximum intensity, the screen was removed and the reaction time ascertained as in the preceding tests. The light was then turned off, the animal returned to its place on the table and covered again with the light-tight box. This process was now repeated with each of the other five specimens on the table, after which it was repeated with all six specimens laterally illuminated (fig. 1, B). The Wratten filter used was now replaced by another, and the whole process repeated. This was continued until each of the thirty-one animals was alternately subjected to photic stimulation of the inner surface and the outer surface of the siphon in each intensity, and the reaction time for each animal was recorded.

Fig. 1. A. Apparatus used for illumination of the inner surface of the siphons of *Mya arenaria* and for lateral illumination of excurrent and incurrent siphons separately. B. Apparatus used for lateral illumination of different portions of the siphon. *a*, aquarium; *b*, block of wood; *dr*, dark-room; *lb*, light box; *m*, *Mya*; *mp*, metal plate with an opening for light to pass through; *ms*, mechanical stage; *o*, opaque screen; *s*, screens with openings for light to pass through; *sm*, sheet of metal attached to mechanical stage; *t*, table; *vs*, ventilator shaft; *wvs*, wall of ventilator shaft.

If an average is taken of the results obtained for all the individuals in each intensity and these averages are arranged as in table 3, the results show that reaction to illumination directed into the siphon is more rapid than the reaction to lateral illumination, and more rapid with the siphon open than with it closed. This supports the conclusion reached in the preceding section that the photosensitive tissue is located near the inner surface of the siphon, but it does not support the conclusion that *Mya* does not respond to photic stimulation when the siphons are closed.

When the reaction times are grouped in relation to the size of the animals and the average of each group is arranged as

TABLE 3

Relative effect of lateral illumination of siphons and illumination directed into the siphons; thirty-one animals used

INTENSITY IN M.C.	REACTION TIME, IN SECONDS, WITH			
	Lateral illumination of siphons		Illumination directed into siphons	
	Open	Closed	Open	Closed
22567.8	1.69	2.01	1.50	1.81
2280.4	1.95	2.25	1.62	2.01
228.1	2.26	2.68	1.87	2.28
23.3	2.67	3.13	2.14	2.63
10.9	2.74	2.65	2.30	2.68
2.3	3.43	3.63	2.88	3.32

in table 4, the results again show that the reaction time is shorter for illumination directed into the siphons than for lateral illumination at the same intensity, thus again indicating that the photosensitive tissue is near the inner surface of the siphon. They also support the conclusion expressed in the section on localized photic stimulation, that small animals are more sensitive than large ones; and they show that there is a progressive increase in the reaction time as the animals increase in size.

If the photosensitive tissue is located near the inner surface of the siphon as the results indicate, then one would expect about the same reaction time in large and small individuals if the inner surface of the siphon is equally illumi-

nated. Since, however, the facts show that the smaller animals have a shorter reaction time than the larger ones, the possibility exists that the photosensitive tissue is located somewhere else than near the inner surface of the siphon.

The question then arises: Why, under the conditions which obtained in the preceding experiment, is the reaction time shorter in small specimens than in large ones, with the inner surface of the siphon illuminated? This may be due to the

TABLE 4

Relation between size and sensitivity; with (L) lateral illumination and with (D) illumination directed into the siphons

Length of animals (cm.)		3.25	4.5	5.0- 5.75	6.0- 6.75	7.0- 7.75	8.0- 8.75
Number of animals used		1	2	11	10	4	3
INTENSITY IN M.C.		REACTION TIME IN SECONDS					
22567.8	L	1.0	1.8	1.52	1.77	1.9	2.2
	D	1.0	1.3	1.46	1.52	1.75	1.95
2280.4	L	1.4	1.7	1.89	2.11	2.15	2.5
	D	1.2	1.47	1.54	1.73	1.8	1.75
228.1	L	1.9	2.6	2.01	2.26	2.5	3.05
	D	1.5	1.7	1.63	2.0	2.0	2.2
23.3	L	2.2	2.73	2.58	2.37	3.9	3.55
	D	1.7	1.95	2.22	2.17	2.35	2.7
10.9	L	2.6	2.85	2.58	2.70	3.35	4.0
	D	2.1	2.1	2.26	2.42	2.25	2.7
2.3	L	2.9	3.1	3.63	3.56	3.3	4.3
	D	2.8	2.8	2.96	2.88	2.83	-

following: the photosensitive tissue may be so located that light must pass through a greater thickness of siphon wall in the large specimens to strike it; the photosensitive tissue illuminated in the various animals may be more sensitive in small specimens than in larger ones; or a greater quantity of photosensitive tissue may have been illuminated in the small individuals than in the large ones.

In subjecting animals to localized photic stimulations, an area having a diameter of 1 mm. in the small animals represents a relatively larger portion of the siphon than in the

large animals. Besides, different animals have the siphon extended to various lengths. A large animal with the siphon slightly extended probably has relatively as much photosensitive tissue exposed in illumination of an area of a given size as a smaller animal with the siphon extended to a greater length.

In order, then, to ascertain whether or not the difference in reaction time was due to illumination of relatively unequal quantities of photosensitive tissue in the different animals, specimens differing in size were subjected to photic stimulation, with relatively equal portions of different regions of siphon exposed to illumination.

Response to light with relatively equal portions of siphons exposed to illumination. In subjecting the animals to lateral illumination in previous experiments, the entire siphon of the small animals and the large contracted ones were often entirely illuminated, while only a portion of the siphon of the large expanded animals was illuminated. To avoid illuminating relatively unequal portions of the siphons of the various animals, the apparatus shown in figure 1, B, was used. This apparatus contains a mechanical stage, to which a piece of sheet metal was fastened, so that by moving the thumbscrew on the stage, the size of the opening through which the beam of light passes can be regulated; and by referring to the scale of the stage, the relative size can be ascertained.

If it is true that *Mya* can extend its siphon to twice the length of the shell (Woodward, '80; Sharp, '84), twice as large an area should be exposed to illumination when fully extended as when half extended, in order to have an approximately equal quantity of photosensitive tissue exposed to the light. In the following observations the width of the beam was, by means of the mechanical stage, so adjusted for each specimen that one-tenth of the length of the siphon was exposed in each test.

In this way regions at the base, the middle, and the very tip of the siphon were subjected to illuminations of different

intensities. In some tests in the high intensities, an equal area of water surface at a point just to one side of the tip of the siphon was illuminated, no direct rays of light striking the siphon. Then, too, for comparison, relatively much larger areas at the tip of the siphon were exposed both to lateral illumination and to illumination directed into the siphons.

The results obtained are presented in table 5. They show that few responses were obtained with illumination at the middle, and practically no responses when the base of the siphon was illuminated. This indicates that the wall of the

TABLE 5

Relation between intensity of illumination and the average reaction time when relatively equal portions of different regions of siphon are exposed to lateral illumination; to illumination directed into the siphons; and to illumination of the water alone near the tip

INTENSITY IN M.C.	REACTION TIME (SECONDS) TO					
	Lateral illumination of					Illumination of inner surface of siphon
	Portion of			Water only	Entire tip	
	Base	Middle	Tip			
4.5	N	N	4.1	—	3.94	4.4
22.8	—	—	—	—	3.41	3.87
44.8	N	N	3.4	—	3.16	3.48
448.1	N	3.2	2.91	5.5	3.01	2.87
4615.8	N	3.85	2.83	3.25	2.73	2.62
44812.1	3.8	3.1	2.41	3.5	2.33	2.20

N, no response; —, no stimulation.

siphon absorbs much of the light, unless the photosensitive tissue diminishes in quantity or in sensitiveness toward the base of the siphon. The table also shows that in the higher intensities illumination of the water alone near the tip of the siphon called forth a response in almost half of the tests, indicating that light reflected into the siphon caused the response, for such responses were only obtained when the siphons were open. Furthermore, it will be seen that, as previously stated, illumination of the inner surface of the siphons results in a shorter reaction time than lateral illumination of the tip; that illumination of the water alone near

the tip calls forth a response in approximately the same time as illumination of the middle of the siphon; and that illuminating a large area of the tip produces a more rapid response than when a small area is illuminated.

These facts again indicate that the photosensitive tissue is near the inner surface of the siphon, but that if it extends the entire length of the inner surface of the siphon, the wall of

TABLE 6

Relation between size of area illuminated and response. Fifteen animals used

SIZE OF ANIMAL (CM.)	DESIGNATION OF ANIMAL	REACTION TIME (SECONDS) TO LATERAL ILLUMINATION AT TIP OF SIPHON	
		Figures taken from individual readings used in preparing table 3; intensity 10.9 m.c. (4 cm. of siphon illuminated)	Figures taken from table 2, in an intensity of 12.4 m.c. (circular area 1 mm. in diameter illuminated)
5.5	6	2.4	2.4
5.5	9	2.45	3.8
5.5	10		2.4
5.5	29		3.2
5.5	51	2.3	
5.5	52	2.85	
5.25	50	2.3	
5.0	11		3.8
5.0	12		3.1
5.0	22		2.4
5.0	28		3.0
5.0	46	2.0	
5.0	70	2.9	
4.5	8	2.9	4.0
4.5	66	2.8	
Average		2.54	3.12

the siphon absorbs most of the rays of light in the larger animals; and that, if this is true, the responses to illumination at the middle and base of the siphon are probably due to the effect of light reflected into the open siphons, as indicated by the responses obtained with the water only illuminated.

The fact that illuminating a large area laterally at the tip of the siphon calls forth a response in less time than illuminating a small area is supported by the results in table 6. The

figures in this table were obtained from table 2, in which small circular areas 1 mm. in diameter were illuminated in an intensity of 12.4 m.c., and from the individual readings used in preparing table 3, in which the entire distal end of the siphon to a point about 4 cm. from the tip was illuminated in an intensity of about 10.9 m.c. The animals selected for comparison varied in length between 4.5 and 5.5 cm., inclusive. Only those readings were recorded in which responses to illumination were obtained with the siphons open. This table shows that the average reaction time with the smaller area exposed was 3.12 seconds, while with the larger area exposed in approximately the same luminous intensity it was only 2.54 seconds, thus indicating that the time required for response is dependent upon the quantity of photosensitive tissue illuminated.

The results presented in the preceding paragraphs show that the reaction time is dependent upon the intensity of illumination; the location of the photosensitive tissue; and the quantity of photosensitive tissue exposed to illumination; and that in the larger animals, when relatively equal portions of siphons are subjected to lateral illumination, there is an increase in the reaction time as the location of the stimulus proceeds from the tip toward the base.

The fact that an increase in the reaction time is obtained as the location of the stimulus proceeds from the tip toward the base of the siphon indicates either that the photosensitive tissue diminishes in quantity or quality toward the base of the siphon or that the siphon wall increases in opacity. In order, then, to ascertain which of these obtains, the response to light in specimens with various portions of the siphons removed was investigated.

B. Operated animals

Response to light with various portions of siphon removed. Animals that have been kept in aquaria in the laboratory under normal conditions usually have their siphons considerably extended. Such animals can be lifted and transferred to

another container with but little contraction, but if the siphon is touched or merely jarred, it usually contracts suddenly. To cut off a definite portion of the siphon, it was therefore thought necessary to anaesthetize the animals.

Two per cent solutions of either cocaine or benzyl alcohol⁵ injected into the siphon wall by means of a hypodermic needle produced local anaesthesia, but the portions of the siphons cut off were to be used for histological study later, and it was not known what effect the anaesthetic might have on the cell structure, and moreover, many animals died from the effects of the anaesthetic. An attempt was therefore made to operate on the siphons without the use of an anaesthetic.

Specimens with their siphons considerably extended were selected for operation. Each animal was carefully placed in a shallow pan, then the siphon was suddenly cut off with a sharp pair of scissors. These specimens withstood the effects of the operation very much better than those which were anaesthetized. Of twelve which were operated several times each, all recovered from the effects of the first, five from the effects of the second, three from the effects of the third, and two from the effects of the fourth operation. This operation, consequently, does not appear to be a great shock to the animal.

To ascertain the response to light with various portions of the siphon removed, twelve specimens were selected. Then the response to light with illumination directed into the siphon openings was ascertained for each specimen, after which a quarter of the length of the siphon was removed from each (fig. 4). All were now returned to the aquaria and left a day or two, after which they were again tested for responses to light. Then they were left a week or more, i.e., until they had completely recovered. Half of the siphon was now removed, after which the entire process was repeated as before. In the same way three-fourths of the siphon, and later as nearly the entire siphon as possible, were removed, the response to light being obtained after each operation.

⁵ Benzyl alcohol was first used as an anaesthetic by Macht, '18.

It soon became apparent that only a small number of the original animals selected would be able to survive four successive operations. Therefore, twelve more animals were selected, and in these the siphon was cut off as near the base as possible. After recovery, it was found that all of the animals had various sizes of short stumps of siphons remaining, one of which was about a quarter of the original length. The response to light was now obtained for this animal, after which as nearly the entire siphon as possible was removed; then the responses to light of all of the specimens were obtained. The results obtained are presented in table 7. These results show that the shortest reaction time in all but

TABLE 7

Relation between the reaction time of all animals and the intensity of illumination; with siphons open; and with various lengths of siphon removed

QUANTITY OF SIPHON REMOVED	NUMBER OF ANIMALS USED	REACTION TIME, IN SECONDS, IN THE FOLLOWING INTENSITIES IN M.C.					
		49907.0	4649.7	501.8	47.4	23.5	5.0
None	12	1.78	2.01	2.17	2.55	2.61	3.23
One-fourth	12	1.65	1.91	2.24	2.81	3.06	3.57
One-half	5	1.54	1.68	1.92	2.34	2.38	3.32
Three-fourths	4	1.6	1.8	1.92	2.3	2.52	3.85
Entire	12	2.85	2.83	3.38	4.7	N	N

N, no response to stimulation.

two intensities was obtained when approximately half of the siphon was removed, and in both of these it was shorter than under all other conditions, excepting when three-fourths of the siphon was removed. The table also shows that, with the siphons entirely removed or nearly so, the reaction time was considerably longer than it was with any other portion of the siphons removed. In the majority of tests under these conditions no response was observed at any luminous intensity, and in those in which responses were obtained it was invariably found that the siphon of the specimen tested was not entirely removed. As a matter of fact, it seemed evident that the longer the stump, the more likely the individual was to respond.

In the preceding sections of this paper evidence was presented which shows that illumination of the inner surface of the siphon produces more rapid response than lateral illumination, thus indicating that the photosensitive tissue lies somewhere near the inner surface of the siphon, and that it extends throughout the length of the siphon. The results here presented support these conclusions, but, contrary to the conclusion reached in the preceding section that the tip of the siphon is most sensitive, they show that the middle portion is most sensitive. If this is true, there must either be more photosensitive tissue at the middle than elsewhere or the tissue that is there must be more sensitive to illumination than that found in other parts of the siphon.

Further evidence concerning the location and quantity of photosensitive tissue in the various parts of the siphon will be presented in the section on a histological study of the siphons.

Regeneration. In order to ascertain whether or not regeneration of the siphon takes place in *Mya*, a portion was removed in several specimens, after which they were put into the aquaria from which they had been taken. These animals were examined with a hand lens from time to time, a few of them for a period of several months, and they were occasionally tested for reaction to light.

The stumps healed completely within a few days. New tentacles formed around both the incurrent and excurrent siphon openings in about a month. The new tentacles developed directly from the new tissue formed in the healing of the wound. The regenerated tentacles were very small at first, but they grew, until in two months they were as long as the tentacles on normal specimens of the same size. Regeneration was, however, confined to reformation of new tentacles. There was no indication of increase in length of the siphon.

The results presented in table 8 are typical of those obtained after regeneration occurred. These results show that the reaction time after regeneration is practically the

same as that immediately following the operation, i.e., that it does not increase while regeneration is taking place. This indicates that there is no regeneration of photosensitive tissue, although there is regeneration of new tentacles. This conclusion was confirmed by a histological study of regenerated tissues, for in no case was photosensitive tissue found in regenerated parts.

TABLE 8

Relation between sensitivity and regeneration in specimen 24 before removal of siphon, soon after its removal, and after regeneration; operation performed September 25th; animal died December 15th

INTENSITY IN M.C.	REACTION TIME (SECONDS)			
	Before operation Sept. 25	After operation Sept. 27	After regeneration	
			Nov. 16	Dec. 10
53114.7	1.2	N	N	2.2
5457.2	1.4	2.8	N	N
505.4	1.6	N	N	N
51.1	1.9	N	N	N
24.5	2.1	N	N	N
5.2	2.3	N	N	N

N, no response obtained.

DISTRIBUTION AND STRUCTURE OF PHOTOSENSITIVE TISSUE AS INDICATED BY A STUDY OF THE STRUCTURE OF THE SIPHON

Distribution of nerves in the siphon

Information in the literature concerning the nerves in the siphon of *Mya* is very meager. By far the best description is given by Duvernoy ('54). In his drawing he represents two excurrent and two incurrent siphon nerves which are distinguished from each other, but he gives nothing concerning the finer details of these nerves and the endings of the fibers. Rawitz ('87) discusses the nervous system of *Mya*, but he figures only two nerves running to the siphon, and he gives no details concerning these. Essentially the same is shown in a drawing by W. R. Brooks, published in Packard's *Zoölogy* ('89).

The siphon nerves were studied both in gross dissection and in serial sections. For the dissection of the larger nerves, the animals were placed in a 4 per cent solution of ethyl alcohol. After a few hours, they were partially anaesthetized and the siphons were considerably extended and expanded; formalin was then added in small quantities until it reached a strength of about 10 per cent. In this solution they were kept until they were used in dissection. Before dissection they were washed in running water until nearly all the formalin was removed.

In dissecting the siphons they were slit lengthwise the entire length, along the midventral side of the incurrent siphon, and along the septum separating the incurrent and excurrent siphons; and then pinned down on a tray partly filled with wax, after which all the large nerves were dissected from the surrounding tissue.

For detailed dissection of smaller nerves, the method employed on earthworms by Hess ('25) was used. Small portions of the siphon were pinned open under water in Petri dishes partly filled with wax. The water was then drawn off and several drops of 2 per cent osmic acid placed on the region to be dissected. The dishes were covered to prevent the acid fumes from escaping, and left for about 10 minutes. At the end of this time, all the nerves on or near the surface were black, so that under a binocular microscope they could easily be dissected from the surrounding tissue. Since only the exposed portions of nerves are affected by the osmic-acid treatment, the process was repeated as often as necessary until dissection was complete.

Methylene blue was also used in dissection. Small pieces of tissue were placed in a Petri dish and covered with a methylene-blue solution (1 gram in 1000 cc. H_2O). After remaining in the stain for ten to fifteen minutes, the pieces were washed in water and then placed in a normal salt solution and dissected as described above. After a short time, however, the stain washed out, and no successful methods to make it permanent were found.

The methods used in the preparation of serial sections will be discussed presently.

The visceral ganglia in *Mya arenaria* lie side by side on the anteroventral side of the posterior adductor muscle, and are so closely associated that they appear as one ganglion (fig. 2).

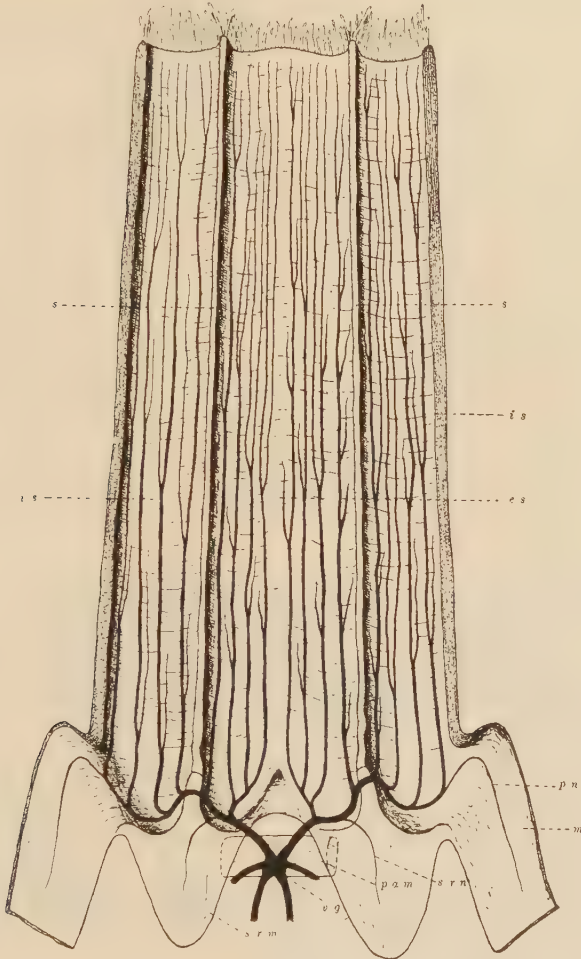


Fig. 2 Drawing showing the arrangement of the larger nerves in the siphon of *Mya arenaria*. The incurrent siphon and the septum separating the incurrent and excurrent siphons are slit lengthwise, and the siphon chambers are laid bare. *is*, incurrent siphon; *es*, excurrent siphon; *m*, mantle; *pam*, posterior adductor muscle; *pn*, pallial nerve; *s*, septum separating incurrent and excurrent siphons; *srm*, siphon retractor muscle; *srn*, siphon retractor nerve.

Each of the two ganglia sends a large nerve trunk posteriorly into the corresponding side of the animal. Each trunk soon divides, one part continuing posteriorly into the corresponding half of the excurrent siphon, while the other part continues as the pallial nerve, passing along between the siphon and the siphon retractor muscle, and bends anteriorly on the ventral side of the animal, innervating the corresponding half of the fused mantle. Soon after dividing, the pallial nerve gives off a small branch which passes anteriorly into the siphon retractor muscle. Five large branches are sent off posteriorly from the pallial nerve. One of these goes to the excurrent siphon near the wall separating the two siphons, and the other four to the incurrent siphon. That portion of the nerve trunk leaving the visceral ganglion, which upon dividing goes to the excurrent siphon, soon divides and sends off three branches into different parts of its half of the excurrent siphon. Thus each lateral half of each siphon is innervated by four large nerves which are connected directly with the central nervous system. These nerves, sixteen in number, extend the entire length of the siphon and send off branches which complete the innervation of the siphons.

A drawing of the cross-section of the siphon (fig. 3) shows that the main siphon nerves are embedded in the longitudinal muscles of the siphons and lie closer to the inside of the siphon than to the outside. There are no large nerves lying in the wall or septum separating the incurrent and excurrent siphons, but two large nerves on each side of the siphon, lying outside the extremities of this septum, send branches into it at intervals. All of the main nerves lie in a circle, at about the same distance, around the two siphon openings, a trifle more than a third of the distance from the inner wall of the siphon toward the outer wall.

Any part of the body of an animal which possesses as many nerves as the siphon of *Mya* must be capable of much nervous activity. When one remembers that these animals, normally buried in the sand, protrude only the tips of their siphons

above the surface and that because of this habit they can keep in touch with their surroundings only by means of the siphons, then the utility of so great an innervation becomes apparent.

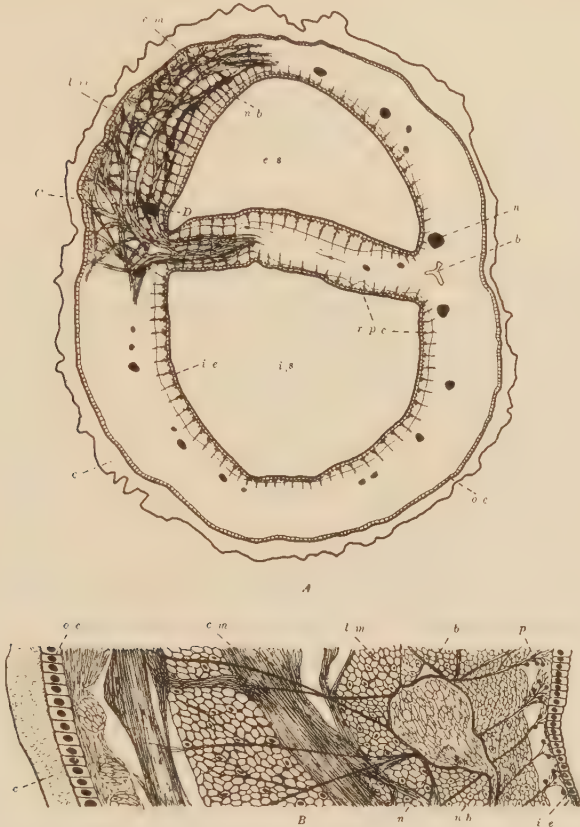


Fig. 3 A. Camera drawing of cross-section of siphon; gold-chloride technique. *b*, blood-vessel; *c*, cuticulum; *cm*, circular muscles; *es*, excurrent siphon; *ie*, inner epithelial cells; *is*, incurrent siphon; *lm*, longitudinal muscles; *n*, nerve trunks; *nb*, nerve branches; *oe*, outer epithelial cells; *p*, photoreceptors; *rpe*, region of photoreceptors. B. Greatly enlarged cross-section of a small portion of the wall of the siphon, through C-D (fig. 3, A), showing relation of photoreceptors and nerves. Labeling same as above.

Histological study of the siphons

Although previous workers, Will ('44), Ryder ('83), Sharp ('84), and Carrière ('85), reported the presence of eyes at

the tip or the base of the tentacles of various molluscs closely related to *Mya*, Leydig ('57) claimed he could not find any eyes in these molluscs.

There is nothing in the literature on the structure of the photosensitive tissue in *Mya arenaria* or in any other closely related mollusc. Kellogg ('92) presents drawings of cross-sections through the body of *Mya* at various places, one through the siphon near the base, but he confines his drawings to gross structure.

For histological study, the best preparations were obtained by using the technique employed by Hess ('25) on earthworms. His method is a variation of Boule's modification of Cajal's silver-nitrate technique. The finer structure of the nerves in the photosensitive tissue was brought out more clearly by this method than by any other. For small nerves and nerve endings, the gold-chloride method as described in Guyer's Micrology was used. The results were satisfactory, but the gold chloride did not penetrate to the deeper tissues in which the principal large siphon nerves are located. Transparent preparations of tissue according to the method of Field ('22) proved very satisfactory in showing the structure of the photosensitive tissue and its connection with the central nervous system. Other material for histological study was fixed with Bouin's, Flemming's, and chrom-aceto-formol fixing fluids, and stained with Mallory's triple connective-tissue stain or Heidenhain's iron hematoxylin. The sections for histological study were cut uniformly 12 μ thick.

A study of the sections shows that the large nerves which extend the length of the siphon send a great number of branches toward the inner part of the siphon. By tracing these branches to their extremities, numerous pear-shaped cells were found, lying just beneath and sometimes in contact with the inner epithelial layer of the siphon. These cells are directly connected with the central nervous system and take on the characteristic silver-nitrate stain for nerve tissue. They are clearly different from any other cells found in the siphon.

The drawing (fig. 3) and the photomicrographs (figs. 8 and 9) show the location of these cells in cross-sections taken a short distance below the tip of the siphon and in a longitudinal section. They lie immediately beneath the inner epithelial layer of both siphons and normally extend entirely around the canals in both, but in fixing and staining, these canals assume a triangular outline in cross-sections, resulting in elimination of the cells at the apices of the angles. They seem to be more numerous in the septum separating the two siphons than elsewhere, although no actual counts were made.

The photomicrograph (fig. 10) shows a highly magnified portion of the section shown in figure 8, taken a short distance below the tip of the siphon. This is a typical section prepared with the silver-nitrate technique (Hess, '25). It shows the pear-shaped cells and their location in the siphons very clearly. These cells are entirely absent in the tentacles.

Distribution of the pear-shaped cells

In order to ascertain the distribution of the pear-shaped cells in the siphon, a histological study was made of ten adjoining serial sections, each 12μ thick, taken from each of the regions designated *A*, *B*, *C*, *D*, *E*, and *F* in figure 4. The pear-shaped cells in all of these sections were counted, and the total number for each of the six regions 120μ thick, taken from different regions of the siphon, ascertained. The results obtained are presented in table 9. These results show that there are more of the pear-shaped cells near the middle of the siphon than elsewhere, that the number diminishes from the middle toward the tip and toward the base, and that at the base there are but few. Sections obtained still farther down than region *F* (fig. 4) contain practically no pear-shaped cells.

By comparing the distribution of these cells with the distribution of sensitiveness in the siphon (table 7), it will be seen that photic sensitivity is definitely correlated with abundance of these cells, the region in which they are most abundant being most sensitive. This correlation strongly indicates that the pear-shaped cells are photosensitive.

Further evidence in support of this conclusion will be presented in the following sections.

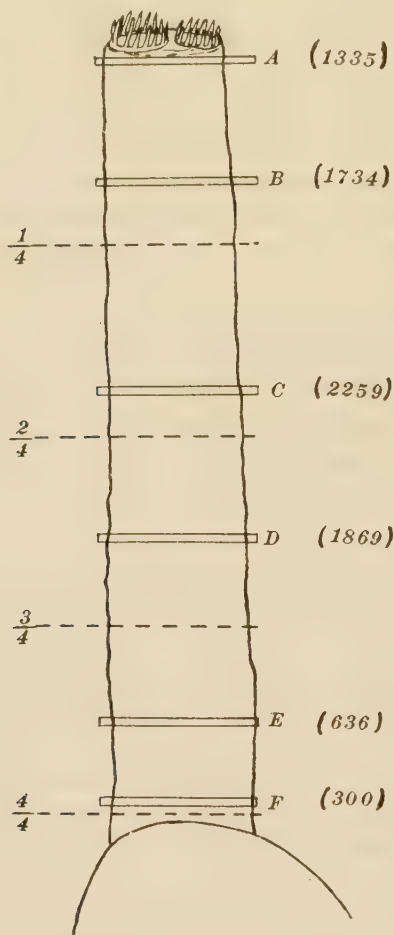


Fig. 4 Drawing of the siphon of *Mya*, showing the location of the regions sectioned (table 11). Figures in parenthesis indicate the number of pear-shaped cells found in ten adjoining serial sections, each 12μ thick, taken from each of the regions designated A, B, C, D, E, and F. Dotted lines indicate the points at which the siphon was cut off in ascertaining the distribution of sensitiveness in it.

Form and structure of the pear-shaped cells

The drawings and description here given are based chiefly on a study of silver-nitrate preparations made with a Zeiss

mono-objective, binocular microscope, $12.5\times$ compensating oculars, and a 2-mm. apochromatic objective. Gold-chloride preparations and preparations stained with Heidenhain's iron hematoxylin following fixation in Flemming's strong fixative or with Mallory's connective-tissue stain following fixation in chrom-aceto-formol fixative were also studied.

The pear-shaped cells found in the siphon of *Mya* vary considerably in size and shape (fig. 5). The variation in size extends from 9 to 15μ in length and from 5 to 10μ in width. As a rule, the longest cells are also the widest, the length being approximately twice the width. Some are, however,

TABLE 9

Distribution of pear-shaped cells as indicated by the number found in ten adjoining sections from each of six different regions in the siphon

LOCATION SHOWN IN FIGURE 4	NUMBER OF CELLS		TOTAL NUMBER, BOTH SIPHONS
	Excurrent siphon	Incurrent siphon	
A (tip)	353	982	1335
B	512	1222	1734
C	995	1264	2259
D	1024	845	1869
E	478	158	636
F (base)	68	232	300
Total	3430	4703	8133

much narrower in proportion to their length (fig. 5, G). Those situated just beneath the epithelial layer vary more than those lying some distance from it.

As a rule, the cells are broadest at the distal end and taper gradually toward the proximal end. Many of the cells are nearly spherical, except for a slight tapering at the proximal end. Most of them, however, are more elongated, being more nearly ovoid. Irregular-shaped cells are found; these are usually embedded in other tissues, and their shape may be due to crowding. Most of the cells have the proximal end bent at an angle of about 45° . This bend in the cell is of considerable importance, as will be explained later.

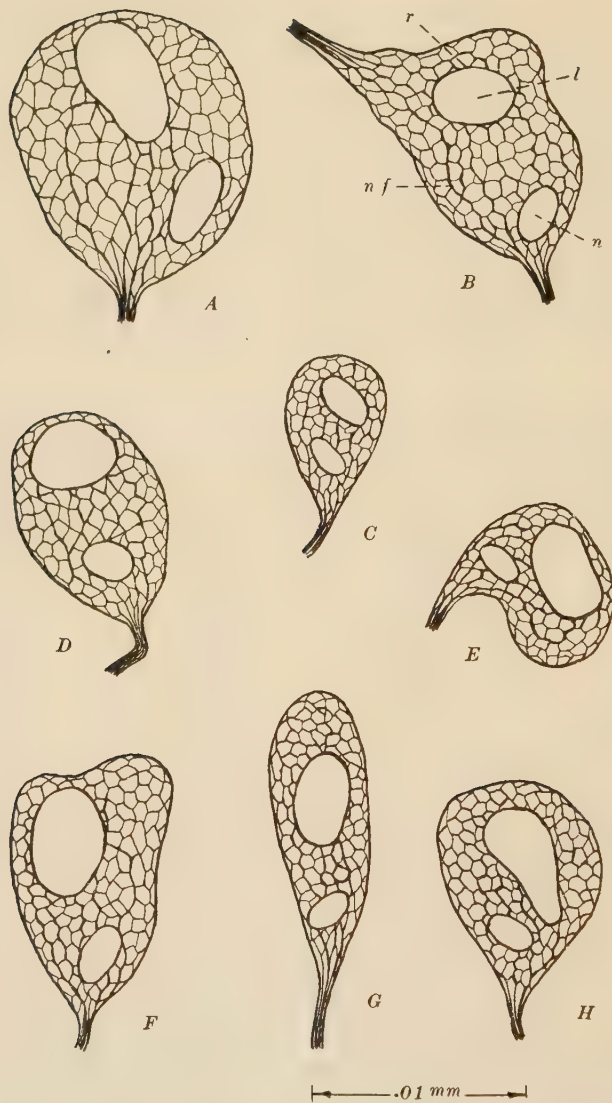


Fig. 5 Camera drawings of longitudinal sections of pear-shaped cells, showing various shapes and sizes. A, cell stained with Heidenhain's hematoxylin; B to H, silver-nitrate technique; B, cell with two fibers. *l*, lens; *n*, nucleus; *nf*, neurofibrils of cytoplasm; *r*, retinella.

As previously stated, these cells are directly connected with the nerves in the siphon. In the silver-nitrate and gold-chloride preparations it can readily be seen that, as a rule, only one nerve fiber enters each cell, although occasionally cells are found which have two fibers entering them (figs. 5, A, and 6, B). These cells are very rare and are only found close to the epithelial layer. The nerve fibers are rather large, as one would expect in cells that possess much nervous activity. Each nerve fiber contains numerous fibrils. It was impossible to follow a fibril from the nerve fiber through the cell, for the

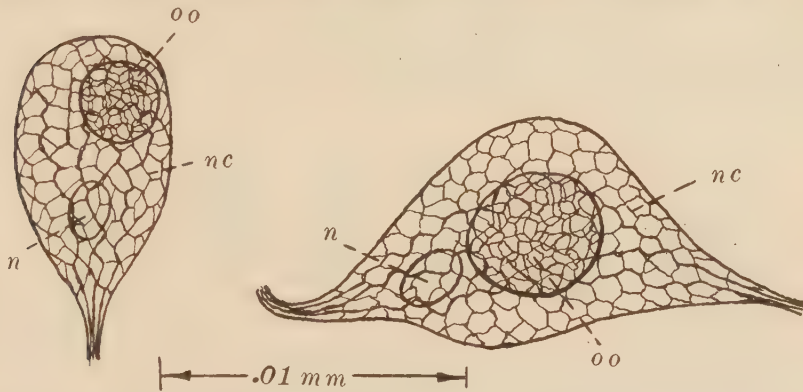


Fig. 6 Camera drawing of pear-shaped cells as seen in side view; silver-nitrate technique. *n*, nucleus; *nc*, neurofibrils of cytoplasm; *oo*, optic organelles.

fibrils appear to branch and anastomose so as to form a rather dense network extending throughout the entire cell.

A rather large nucleus is found, usually lying near the proximal end of the cell. There is no indication of any neural structures connected directly with it. The cytoplasm, aside from the fibrils, appears homogeneous in the silver-nitrate and the gold-chloride preparations, but it has an alveolar appearance in hematoxylin and in Mallory's connective-tissue preparations.

The most conspicuous feature of the pear-shaped cells is a large intracellular structure, lying near the surface, at the distal end. This structure is peculiar to these cells, and is a characteristic by which they can readily be recognized. It

varies in size from 5 to 7 μ in length and from 3 to 5 μ in width. The largest ones are not always found in the largest cells. These structures are sometimes spherical in shape, but they are usually elongated, and somewhat tapering or curved (fig. 7); they are always nearly circular in cross-section.

The surface of this structure presents a very dense appearance in silver-nitrate preparations, which on careful examination can be seen to be due to the presence of numerous, rather large, anastomosing neurofibrils. These neurofibrils are connected directly with those which appear to branch from the fibrils that enter the cell. The inner region of this conspicuous structure is composed of a transparent, hyaline substance, which seems differentiated into zones of different density.

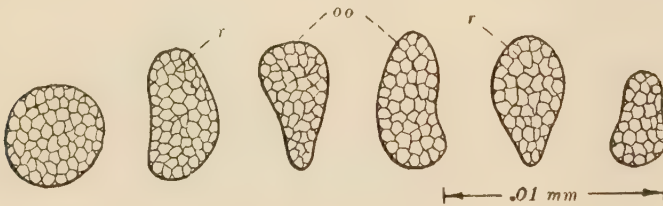


Fig. 7 Camera drawings of several optic organelles, as seen in side view; silver-nitrate technique. oo, optic organelles; r, retinella.

Hesse ('96) found a somewhat similar structure in the earthworm *Lumbricus*, which he called a 'Binnenkörper,' and Apáthy ('97), in the leech *Pseudobranchellion*, which he called a 'Glaskörper.' Apáthy called the cell in which the 'Glaskörper' was found a 'Retinazelle.' He thus suggests that the 'Glaskörper' functions as a lens in a visual organ. Beer ('01), in discussing the 'Glaskörper' of *Pseudobranchellion* described by Apáthy, refers to it as 'Binnenkörper,' using the term first employed by Hesse. Hess ('25) calls these cells photoreceptors, and furnishes evidence which indicates that the 'Binnenkörper' serves to focus rays of light upon the neurofibrils which surround it; he consequently proposed to designate it 'optic organelle.'

Evidence will be presented in the following section to show that the structures found in the pear-shaped cells of *Mya* have

the same function as the optic organelle found by Hess in *Lumbricus*. They will also therefore be called 'optic organelles.'

Function of the optic organelle

Small portions of the septum separating the incurrent and excurrent siphons were dissected from the cut-off tips of recently operated animals, placed under the binocular microscope in normal salt solution, and carefully teased with fine needles. In this way some of the pear-shaped cells were loosened from their nerve attachments. Several of these were transferred by means of a pipette and mounted in a hanging-drop of normal salt solution, others were placed on a glass slide and covered with a cover-glass. The cells thus mounted were placed on the stage of a compound microscope and exposed to illumination from below and from the side. In illuminating from below, the condenser of the microscope was removed and the light reflected up with the plane mirror. Lateral illumination was accomplished by means of a Spencer microscope lamp.

Under a magnification of about 300 diameters, definite focal regions of light are clearly seen. These regions are always on the side opposite that at which the light enters. This region is sometimes small and circular in outline and sometimes elongated, forming a band of light which is never of a greater length than the optic organelle. The focal region is always at the surface of the optic organelles, on the neurofibrillar network which surrounds it, irrespective of the direction in which the light enters the cell. It appears, then, that there is a refracting body in the cell which is of such a nature that it brings light to a focus at the surface of the optic organelle, irrespective of the direction. This indicates that the optic organelle is a lens.

The arrangement of the pear-shaped cells, previously described, so as to lie at an angle of about 45° with a perpendicular to the inner wall of the siphon is of considerable importance in receiving light directed into the siphons, for

more light enters the optic organelles when they are arranged at this angle than when either perpendicular or parallel to the siphon wall.

If the objective of the microscope is slightly raised or lowered, while light reflected from below is focused on the neurofibrillar network of the optic organelle, then the spot of light changes color. When the objective is raised, the spot becomes reddish in color; when it is lowered, the spot has a bluish tinge at its border. This change in color is a common characteristic due to the refraction of light in lenses, and supports the conclusion that the hyaline interior of the optic organelle functions as a lens.

If the hyaline interior of the optic organelle actually focuses the light on the neurofibrillar network surrounding it as maintained above, the neurofibrillar network is probably photosensitive. If it is, it may be designated a 'retinella.' This is in full accord with the conclusion of Hess ('25) concerning the function of the optic organelle in *Lumbricus*. If all this obtains, the pear-shaped cells containing the optic organelles are photoreceptors.

RELATION BETWEEN LOCATION AND DISTRIBUTION OF PHOTORECEPTORS AND THE HABITS OF THE ANIMALS

We have seen that the photoreceptors are located near the inner epithelial layer of the siphons. This is where one would expect them, considering the habits of the animal.

Mya in its natural habitat lies embedded in the sand or mud, with the siphon perpendicular to the surface. The outer wall of the siphon is entirely surrounded by the sand or mud, and it would be almost impossible for photoreceptors to function if they were located near this wall. The tip of the siphon is just about on a level with the surface, and when it is open, the inner walls of the siphon are exposed to rays of light from above.

When the animal is disturbed in any way, it suddenly contracts, withdrawing the tip of the siphon and closing the openings. This contraction is sufficient to withdraw the tip of the

siphon from immediate reach of enemies. Having withdrawn within its burrow, there is no need for photoreceptors, for any attempt to reach the animal must of necessity disturb the surrounding sand, thus warning the animal through its sense of touch. Before the siphons are extended, they are opened, then they are slowly extended to the surface. This procedure one would expect in animals that have the photoreceptors located on the inside of the siphon, for if they were located in the tentacles or near the outer surface, there would be no need for opening the siphon before extending it.

Piéron ('25) claims that *Mya* lies buried in the sand and mud during the day, and extends its siphon above the surface of the sand at night to feed. If this is true, the photoreceptors seem to function in keeping the siphon from exposure during the day, when most enemies are active.

Tryon ('82), Lovell ('67), Ingersoll ('87), Kellogg ('10), and others state that the enemies of *Mya* consist of the walrus, the Arctic fox, cormorants, gulls, crows, etc., and various kinds of fishes. From personal experience nothing is known concerning this except the following: Crows were seen walking along the edge of the water at low tide during the winter season, when food was scarce because of a blanket of snow on the ground; and upon going to the spot where the crows had been, there were found numerous indications of small specimens of *Mya* recently pulled out of their burrows, their shells crushed, and edible portions eaten. In one instance a medium-sized *Mya* was found, exposed to the cold air and benumbed by it, with the tender tip of the siphon picked off by a crow. The tracks of the crow were clearly visible in the sand, and the crow itself was seen at that spot a short time before.

If the loss of tips of siphons as described above is a regular occurrence, then the fact that the photoreceptors are distributed along the entire inside of the siphons is of considerable importance to these animals, for with such distribution a portion of the siphon might be removed by an enemy, and the remnant would still function.

RELATION OF PIGMENT SPOTS TO PHOTORECEPTORS

As stated by Ryder ('83) and Sharp ('84), pigment is found on the upper end of the siphon of *Mya*, both inside and outside, and lines of pigment are found around the base of the tentacles. Ryder claims to have found it in the epidermis and beneath it. In my preparations no pigment was found under this layer. Pigmented cells were found at various places in groups, as stated by Sharp, but these groups were not found in particularly protected places as Sharp contends. They are fairly regularly arranged on the entire surface of the tip of the siphon.

Most previous workers contend that the presence of pigment near the tip of the siphon indicates that there are visual organs in *Mya*, for in many instances it is well known that visual organs and pigment are closely associated. In my preparations, however, no relation was found between the pigmented areas and the photoreceptors. The pigmented areas are more numerous near the tip and do not extend any considerable distance down along the inside of the siphon, while the photoreceptors are found all along the entire inner wall of the siphon.

The probable value of pigment spots on the siphon of *Mya* lies not in its function in photoreception, but in its ability to more nearly simulate the background through which the tip of the siphon protrudes. The spotted tip of the siphon closely resembles grains of sand surrounding it, thereby escaping detection and thus affording protection from enemies.

SUMMARY

If *Mya* is subjected to a sudden increase in illumination, it responds with a marked contraction of the siphon.

The reaction time decreases as luminous intensity increases.

It is shorter with illumination directed into the siphon than in lateral illumination of the same intensity. The inner surface is more sensitive than the outer.

It is shorter when large areas are illuminated than when small areas are illuminated in the same intensity.

It is shorter in small than in large animals.

The siphon is sensitive throughout its entire length. The middle portion is most sensitive, the sensitivity decreasing from the middle toward the tip and toward the base, becoming practically zero at the base.

Regeneration of tentacles on stumps of severed siphons takes place, but there is no regeneration of other tissues.

Eight large nerves, extending the entire length of the siphon and lying closer to the inner siphon wall than the outer wall, surround both the incurrent and the excurrent siphon.

Pear-shaped cells that take on stain for nerve tissue are found beneath the inner epithelial layer in the siphon, but not in other parts of the siphon.

The distribution of these cells in the siphon is closely correlated with the distribution of sensitivity in reference to photic stimulation.

Each of these cells is supplied with a large nerve fiber, and each contains a characteristic structure, which is similar to that found by other investigators in other forms designated 'Binnenkörper,' 'Glaskörper,' and 'optic organelle.'

This structure we will call optic organelle. The inner portion of it is hyaline; it refracts light and focuses it upon a neurofibrillar network, the retinella, which surrounds it.

The optic organelles vary considerably in size and shape, but they always appear circular in cross-section.

The pigmented spots found both on the inside and the outside of the siphon in *Mya* have no relation whatever with the position and function of the pear-shaped cells. They probably function in simulating the background, thus protecting the siphon against enemies.

The distribution of photoreceptors along the entire inside of the siphons is of considerable importance to these animals, for with such distribution, if a portion of the siphon is removed by an enemy, the remainder can still function.

The photoreceptors found in the earthworm and the visual cells found in the leech appear to be homologous with the pear-shaped cells found in *Mya*.

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PLATE 1

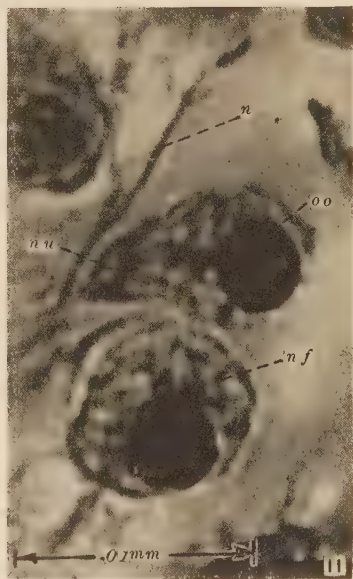
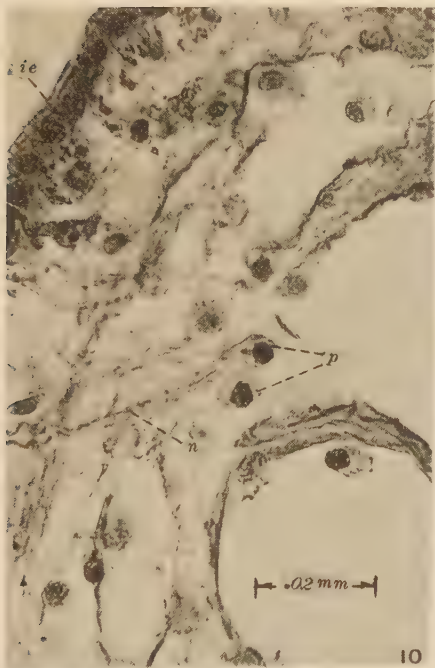
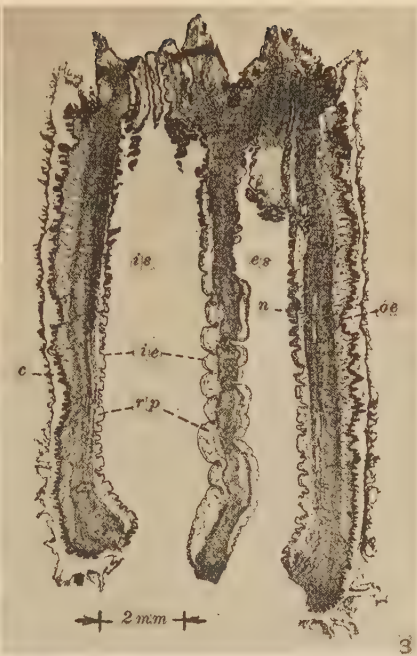
EXPLANATION OF FIGURES

8 Photomicrograph of a longitudinal section through the tip of the siphon of *Mya*, perpendicular to the septum; silver-nitrate technique. *c*, cuticulum; *es*, excurrent siphon; *ie*, inner epithelial layer; *is*, incurrent siphon; *n*, nerve; *oe*, outer epithelial layer; *rp*, region of photoreceptors.

9 Photomicrograph of a cross-section through tip of *Mya* siphon, about 1 cm. from the tentacles; silver-nitrate technique. Labels same as for figure 8.

10 Photomicrograph of a portion of the septum of *Mya*, in the region of the photoreceptors; silver-nitrate technique. *ie*, inner epithelial layer; *n*, nerve fibers; *p*, photoreceptors.

11 Photomicrograph of two photoreceptors shown in figure 10; silver-nitrate technique. *n*, nerve fiber; *nf*, neurofibrils; *nu*, nucleus; *oo*, optic organelle.



VITA

Vernal Earl Light was born in Lebanon County, Pennsylvania, January 9, 1892. He attended the public schools of Pennsylvania, graduating from the High School at Annville in 1908. The next year was spent at Lebanon Valley Academy, completing the requirements necessary to enter Lebanon Valley College, Annville, Pennsylvania. He completed the first year of the college course at this place in the spring of 1910, and spent the next three years, 1910-1913, teaching an ungraded country school in Lebanon County. He returned to Lebanon Valley College, and continued work as a student until January, 1916, and taught the rest of the year in the Lebanon High School. He received the degree of Bachelor of Arts in absentia from Lebanon Valley College in June, 1916. The following years, 1916 to 1926, were spent as a teacher of sciences in various high schools in Pennsylvania. At various times during this period he took extension courses at Lebanon Valley College, attending two summer sessions, and was awarded the degree of Master of Science in June, 1926. He was a graduate student in zoölogy in the Johns Hopkins University three years, beginning in the fall of 1926. The first year he was graduate assistant; the second, student technician; and the third, he held a Hopkins scholarship. The summer of 1926 was spent as a student in the field zoölogy course at the Biological Laboratory, Cold Spring Harbor, Long Island; the summer of 1927, in investigation at the Marine Biological Laboratory, Woods Hole, Massachusetts; and the summer of 1928, in investigation at the Johns Hopkins University.

